SHOOT MORPHOLOGY IN THE *CLAYTONIA SIBIRICA* COMPLEX (PORTULACACEAE)

Robin O'Quinn[1,2] and Larry Hufford
Washington State University, School of Biological Sciences Pullman, WA 99164-4236

Abstract

The *Claytonia sibirica* complex, including *C. sibirica* and *C. palustris*, exhibits considerable morphological variation that encompasses ecological diversity over a wide geographic range. Shoots are basically rhizomatous in the complex and least specialized in *C. sibirica* var. *sibirica*. *Claytonia sibirica* var. *bulbillifera*, a serpentine endemic of southern Oregon and northern California, forms succulent, storage scale leaves distal to its foliage leaves each growing season. These scale leaves, which consist primarily of leaf base, are generally lacking in other members of the sibirica complex and give the shoot systems of *C. sibirica* var. *bulbillifera* a bulb morphology. *Claytonia palustris*, like *C. sibirica* var. *sibirica*, forms an apically swollen rhizome, but differs in its habit by forming renewal shoots, born in the axils of the basal leaves, at the ends of plagiotropic, single long internodes.

Key Words: Bulb, homology, leaf specializations, perennation, shoot architecture, serpentine.

The *Claytonia sibirica* L. complex consists of understory herbs of coastal and mesic inland forests extending from northern Santa Cruz County, California, to coastal northeastern Siberia (Miller et al. 1984; Chambers 1993; Miller 2003). The *C. sibirica* complex consists of annuals and perennials that exhibit considerable morphological, ecological and cytological variation over its range. Shoot systems in the *C. sibirica* complex have been most often described as rhizomatous, although shoot system specializations associated with geographic and ploidy variation have been described.

In the Klamath region (KR) of northwestern California and southwestern Oregon, *C. sibirica* have specialized underground structures involved in perennation (Gray 1877, 1887; Miller et al. 1884). Gray (1877) first described this KR form as *C. bulbifera* Gray and suggested it resembled *C. sibirica* but produced densely crowded perennating bulbs in a basal rosette. However, Gray's (1887) revision of the North American Portulacaceae treated *C. bulbifera* as *C. sibirica* L. var. *bulbillifera* Gray and described it as "...only a form of *C. sibirica* with thickened bases of the radical leaves, which persist on the crown as bulblet-scales."

Miller et al. (1984, p. 266) suggested that the *C. sibirica* complex consists of three basic morphotypes that differ in "shape of basal leaves and the presence or absence of basal bulblets and rhizomes". Gray's (1877, 1887) *C. sibirica* var. *bulbillifera* represents one morphotype recognized by Miller et al. (1984), which they characterize as

bulbiferous, distinguished by elliptical basal leaves, and geographically localized to southern Oregon and northern California where it occurs frequently on serpentine substrates (Fig. 1). We will use this name to refer to the specialized KR morphotype. A second morphotype recognized by Miller et al. (1984) is found in shaded mesic habitats and has the deltoid basal leaf shape of
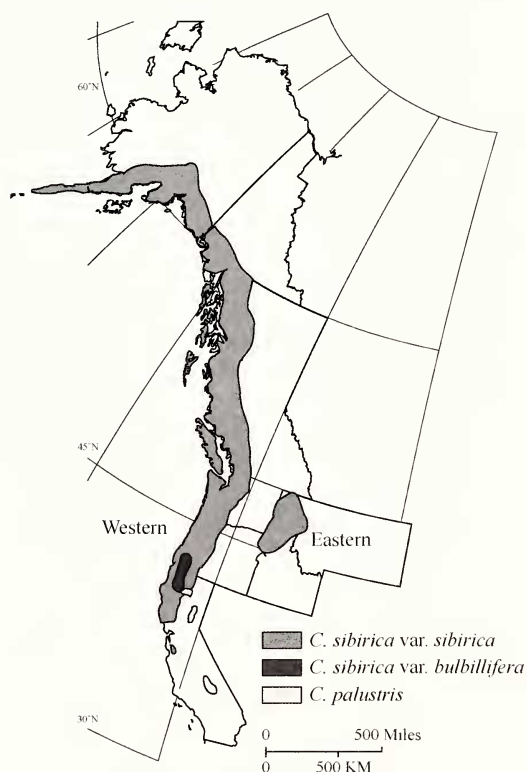

FIG. 1. Geographic distribution of the *Claytonia sibirica* complex.

[1] Author for correspondence, e-mail: oquinn@pdx.edu
[2] Present address: Portland State University, Department of Biology, Portland, OR 97208
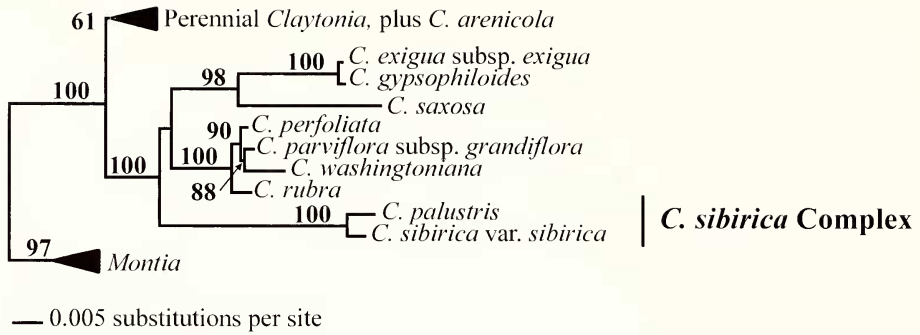
FIG. 2. Maximum likelihood cladogram from combined ITS and *trnK/matK* data showing phylogenetic relationships of the *Claytonia sibirica* complex from O'Quinn and Hufford (2005).

the type specimen for *C. sibirica* var. *sibirica*. We apply the name *C. sibirica* var. *sibirica* to populations distributed in the Pacific Northwest along the Cascadian cordillera, the Columbia River Gorge, coast ranges northward from Santa Cruz county, California, to Alaska, and the Aleutian and Commander Islands (Fig. 1). It overlaps with *C. sibirica* var. *bulbillifera* in the KR (Fig. 1). *Claytonia sibirica* var. *sibirica* also has disjunct populations in the inland Northwest (northern Idaho, western Montana and surrounding portions of Oregon and British Columbia; Fig. 1). We distinguish the morphological variation in *C. sibirica* var. *sibirica* as western and eastern morphotypes. Miller et al. (1984) characterized *C. sibirica* var. *sibirica* as bulbiferous also, but less so than the endemic KR morphotype (=*C.sibirica* var. *bulbillifera sensu* Gray 1887). The disjunct eastern populations of *C. sibirica* var. *sibirica* are reported to lack swollen leaves. The third morphotype discussed by Miller et al. (1984) was later described as *C. palustris* by Swanson and Kelley (1987). *Claytonia palustris* is narrowly endemic to two small, mid-elevation regions at the northern and southern ends of the Sierra Nevada and in Siskyou County, California, where it overlaps with *C. sibirica* var. *bulbillifera* at the eastern edge of its range (Fig. 1). This taxon is unique in the complex in preferring perennially wet, sunny habitats and was described by Swanson and Kelley (1987) as being strongly stoloniferous.

O'Quinn and Hufford (2005) found robust support for the monophyly of the Miller et al. (1984) *C. sibirica* complex based on plastid and nuclear ribosomal DNA sequence data (Fig. 2). Notably, all members of the complex share a unique 10 base pair motif that includes a three-base pair insertion in the internal transcribed spacer region of the nuclear ribosomal DNA. Phylogenetic results recovered a sister taxon relationship between *C. palustris* and *C. sibirica*, but lineages within *C. sibirica* were not resolved.

In this study we characterize shoot morphology of the *C. sibirica* complex, with a particular emphasis on specializations for nutrient storage and perennation. Beyond Gray's (1877) initial description of *C. sibirica* var. *bulbillifera*, the morphology of the so-called bulbiferous morphotype of the KR populations has not been studied previously. This comparative study of the shoot systems in the *C. sibirica* complex addresses especially the morphological identity of structures described as bulbs and bulbiferous and presents hypotheses for the origins of morphological specializations.

MATERIALS AND METHODS

We sampled specimens of the western morphotype of *C. sibirica* var. *sibirica* from the Williamette Valley, Columbia River Gorge and foothills of the Hood River valley, and of the eastern morphotype from the Lochsa and Clearwater River valleys (Table 1). *Claytonia sibirica* var. *bulbillifera* was collected in the Illinois and Rogue River valleys of southern Oregon where this variety is the most common morphotype (Table 1). Samples of *C. palustris* were collected at the type locality at Jones Creek in Butte County, California, and seeds for greenhouse grown material were collected from a population at Stubbs Lake, Butte County, California (Table 1). Based on the cytogeographic results of Miller et al. (1984), we assume that our collections of the eastern morphotype of *C. sibirica* var. *sibirica*, *C. sibirica* var. *bulbillifera*, and *C. palustris* are diploid. Collections of the western morphotype of *C. sibirica* var. *sibirica* are potentially either diploid or tetraploid. Miller et al. (1984) suggested that diploids and polyploids have the same shoot morphologies.

Comparisons of shoot system morphology for the four perennial forms of *C. sibirica* used scanning electron (SEM), and light (LM) microscopy. Specimens from natural, greenhouse and common garden populations were sampled in May or June and August (Table 1) for fixation in formalin-acetic acid (FAA). Specimens for SEM were dehydrated in a graded ethanol series, critical-point dried, and mounted on aluminum stubs prior to gold coating. We examined 5–8

TABLE 1.   COLLECTION DATA FOR SAMPLED POPULATIONS OF THE *C. SIBIRICA* COMPLEX. All vouchers are at WS.

Taxon name	Population location	Collection voucher	Collection date
Claytonia sibirica var. *sibirica* Eastern morphotype	Lochsa River sites: Glade Creek	R. O'Quinn 483	17 May 2002
	Eagle Summit	R. O'Quinn 488	17 May 2002
	Ashpile Creek	R. O'Quinn s.n	25 Aug 2002
Claytonia sibirica var. *sibirica* Western morphotype	Columbia River sites: Herman Creek	R. O'Quinn 492	20 May 2002
		R. O'Quinn 528	19 March 2003
	Bridal Veil Falls	J. Schenk 774	28 June 2004
	Hood River site: Pine Mountain Road	R. O'Quinn 490	20 May 2002
		R. O'Quinn s.n.	31 Aug 2002
		R. O'Quinn 529	19 Mar 2003
		J. Schenk 774	28 June 2004
	Willamette River site: Corvallis, OR	J. Schenk 773	27 June 2004
Claytonia sibirica var. *bulbillifera*	Southern Oregon sites: Davis Creek	R. O'Quinn 494	22 May 2002
	Brigg's Valley Road	R. O'Quinn 504	23 May 2002
	Cave's Camp Road	R. O'Quinn 365	29 May 2001
		R. O'Quinn 474	05 Aug 2001
	Eight Dollar Mtn. Road	R. O'Quinn 290	24 May 2000
		R. O'Quinn 508	24 May 2002
Claytonia palustris	Northern California sites: Jonesville (type location)	R. O'Quinn 330	4 June 2000
	Stubb's Lake (seed source for greenhouse grown collections)	C. Björk 5704b	Multiple collections between 2001 and 2004

individuals per morphotype for SEM. Specimens were examined at an accelerating voltage of 15–20 kV. Images were captured digitally using the program Quartz PCI (Quartz Imaging Corp. 1993–1998). Specimens for LM were dehydrated in a graded tertiary-butyl alcohol series (Johansen 1940), infiltrated and embedded in Paraplast™, sectioned at 16 μm, mounted on glass slides, stained with safranin-O and fast green, and examined with a Leitz light microscope. Microtomed sections were photographed or drawn using a drawing tube. To characterize shoot architecture and leaf base shape over ontogeny, we made cross and longitudinal sections through the basal rosettes of 3–5 individuals per examined population (Table 1) of western and eastern *C. sibirica* var. *sibirica*, *C. sibirica* var. *bulbillifera*, and greenhouse grown specimens of *C. palustris*. Seasonal growth along shoots was identified by discrete regions of leaf scars that differ from each other in length and circumference along a continuous shoot axis.

RESULTS

Shoot Architecture

Claytonia sibirica var. *sibirica*. Perennials form an orthotropic to plagiotropic shoot with short internodes that bear helically arranged leaves, forming a rosette of photosynthetic leaves at the base of the newly elongating axis early in the growth season. Inflorescence branches and renewal shoots form in the axils of the basal leaves (Fig. 3A). The main axis of the shoot enlarges in length to approximately 1–2 cm over the growth season and becomes globose/ovoid (0.5–1.0 cm in diameter) at its distal end (Figs. 3A, 4A); however, shoot size is variable and appears to depend on the age and growth conditions of the individual. Shoots older than one season have a distal globose/ovoid region and a proximal cylindrical region that consists of stem produced in the preceding one or two growth seasons. The main axis of the shoot rarely consists of more than three growing seasons of growth. Some shoots retain their taproot up to their third growth season (Fig. 4B); however, more commonly the younger shoot axes disarticulate from older portions of rhizomes with taproots. The younger shoot axes form shoot-borne roots associated with nodes of the basal leaves.

When a new growth cycle commences, several whorls of foliage leaves expand before the first inflorescences emerge. Each inflorescence has a pair of opposite, sessile leaves (Fig. 4C) and each flower is subtended by a small, oblanceolate bract. Inflorescences develop initially from the axils of the distal leaves in the basal rosette. Subsequently, inflorescences can form in the axils of more proximal leaf positions in the basal rosette, although branches developing in these leaf axils can also form renewal shoots (Fig. 3A).
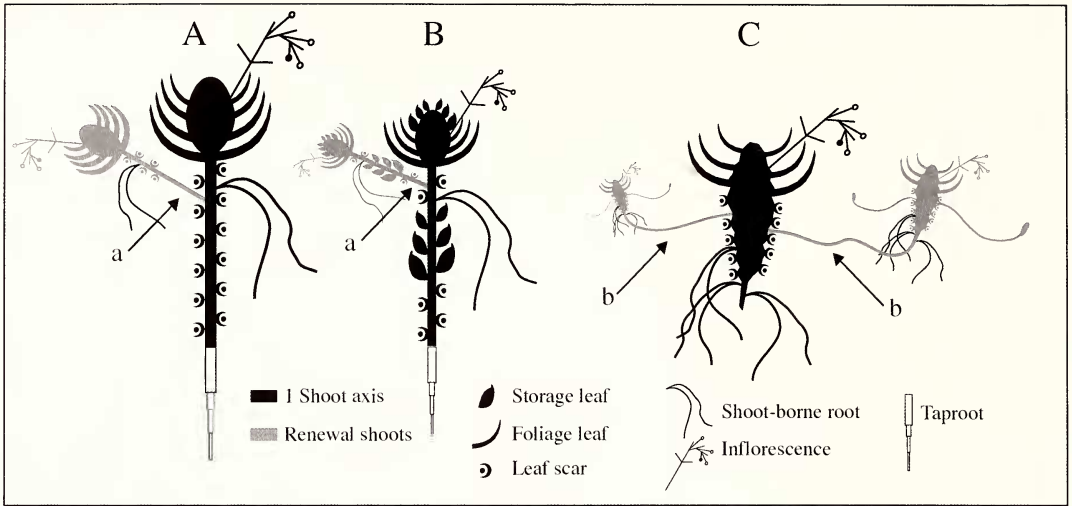
Fig. 3. Diagram of shoot system architecture in the *Claytonia sibirica* complex. A. *C. sibirica* var. *sibirica* B. *C. sibirica* var. *bulbillifera* C. *C. palustris*. Arrows labeled 'a' show aerial rhizomes, arrows labeled 'b' show hypopodia.

Renewal shoots have a basal rosette of helically arranged leaves. Elongation in the lower internodes of these axillary branches (below their rosette of foliage leaves) can create aerial rhizomes that extend renewal shoots 1–5 cm away from the main axis (Fig. 3A). Axillary, aerial rhizomes have shoot-borne roots associated with the nodes of the basal rosette leaves.

In most shoots, all leaves are foliage leaves and have a leaf base, petiole and lamina. Foliage leaves have a range of forms, varying in size depending on growing conditions and probably ploidy level, but range from 3–30 cm in overall length and 5-8 cm in blade width (Fig. 4C). Leaf bases are crescentic in cross-section and the width to thickness ratio increases as they age (Fig. 4D–F). Petioles are terete in cross-section and roughly twice the length of the lamina. The laminas of basal leaves in *C. sibirica* var. *sibirica* are generally deltoid (Fig. 4C); however, Miller et al. (1984) illustrate a wide range of variation in lamina shape in tetraploid and hexaploid populations. Foliage leaf color is consistently bright green for both eastern and western morphotypes.

Some ramets produce late season scale leaves in addition to foliage leaves. The scale leaves consist largely of leaf base and have a rudimentary petiole and lamina (Fig. 4G). This heteroblastic shift occurs uncommonly in populations of the western morphotype of *C. sibirica* var. *sibirica* but was not observed among any individuals from populations of the eastern morphotype.

Claytonia sibirica var. *bulbillifera.* This variety has shoot morphology distinct from that of *C. sibirica* var. *sibirica* in stature, habit, perennation strategy and leaf specialization. Its shallow, subterranean shoot system is consistently smaller than that of *C. sibirica* var. *sibirica*, and its growth habit more lax (Fig. 5A). *Claytonia sibirica* var. *bulbillifera* shoot systems are generally similar to those of var. *sibirica* in producing annually a globose/ovoid, orthotropic axis (Figs. 3B, 5B) that has a basal rosette of helically arranged leaves. Inflorescences form in the axils of leaves in the basal rosette as in *C. sibirica* var. *sibirica*. Renewal shoots that form in the axils of the earliest basal leaves can elongate as rhizomes.

Claytonia sibirica var. *bulbillifera* produces specialized storage leaves that have a swollen, succulent leaf base and an unexpanded petiole and lamina (Figs. 3B, 5C–G) at nodes distal to the foliage leaves in the latter part of the growing season (Fig. 3B). At the beginning of the next growing season, these storage leaves can be either decaying or still turgid (Fig. 5D). With the resumption of shoot growth, the axis thickens and elongates distal to the storage leaf zone, new foliage leaves expand as a basal rosette, and inflorescences elongate from those rosette leaf axils. Foliage leaves have a distinct leaf base, petiole and narrowly to broadly elliptic lamina (Fig. 5A), and they are often gray green with a reddish hue, especially when associated with sunny, serpentine sites. Shoot-borne roots emerge in the region between the storage leaves and the newly expanding foliage leaves. By late spring, storage leaves are produced distal to the foliage leaf zone (Fig. 3B). During the summer, shoot systems of *C. sibirica* var. *bulbillifera* produce a range of leaf types from the typical foliage leaf described above to a modified form of foliage leaf, which has a succulent leaf base and expanded petiole (Fig. 5F) and lamina, as well as storage leaves (Fig. 5C–G). Inflorescences continue to expand from axillary buds of all leaf
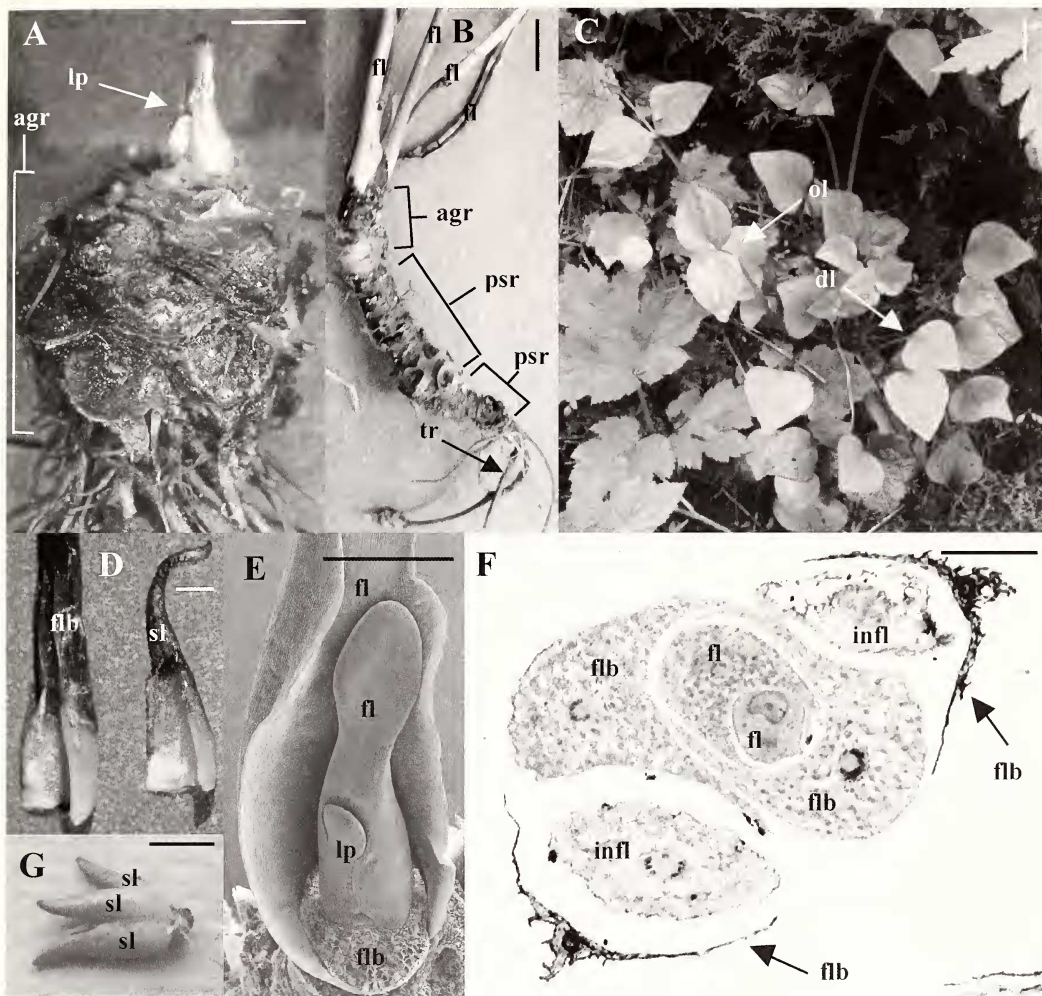
FIG. 4. Shoot system of *Claytonia sibirica* var. *sibirica*. A. Globose/ovoid shoot from active growth phase with foliage leaves and inflorescences removed (western morphotype). B. Shoot system of the eastern morphotype that shows three seasons of growth as discrete regions of leaf scars along a continuous shoot axis and retains a taproot. C. Habit. Arrows show opposite leaves subtending the inflorescence and deltoid lamina of the foliage leaf. D. Leaf base of foliage leaf (left) and scale leaf (right). E. Apex of a shoot system, showing the broad leaf base of a foliage leaf and two developing leaves. F. Cross section through the distal portion of a shoot showing the transectional shapes of leaf bases. G. Scale leaves that formed distally to the foliage leaves. agr = active growth rhizome, dl = deltoid lamina, fl = foliage leaf, flb = foliage leaf base, infl = inflorescence axis, lp = leaf primordium, ol = opposite leaves on inflorescence axis, psr = preceding season's rhizome, sl = scale leaf, slb = scale leaf base, tr = taproot. Scale bar = 3.0 mm in A; 2.0 mm in D, G; 1.86 mm in E; 1.0 mm in F; and 1 cm in B, C.

types throughout the growth season, which is extended for plants growing in more mesic sites. On drier sites, however, the above ground biomass withers and dies by late summer, leaving a shallowly subterranean shoot system that has prominent storage leaves (Fig. 5E). At the end of the growing season, *C. sibirica* var. *bulbillifera* preforms the foliage leaves and inflorescence buds that will expand during the next growing season.

Claytonia palustris. *Claytonia palustris* is shallowly subterranean and often submerged. It differs from the rest of the sibirica complex in habit, degree of internode elongation, vegetative reproduction, production of modified leaves and size. Shoot systems are weakly orthotropic to plagiotropic, consisting of a swollen ovoid stem with alternately arranged, sheathing leaves with dorsiventrally flattened bases. Leaves form in an open basal rosette that has longer internodes and fewer foliage leaves than the rosettes of the sibirica varieties (Figs. 3C, 6A–E). No leaf specializations for storage or perennation were observed in greenhouse grown or field-collected material. Greenhouse grown material grew only vegetatively. Renewal branches form in the axils of the lowermost leaves of the basal rosette and
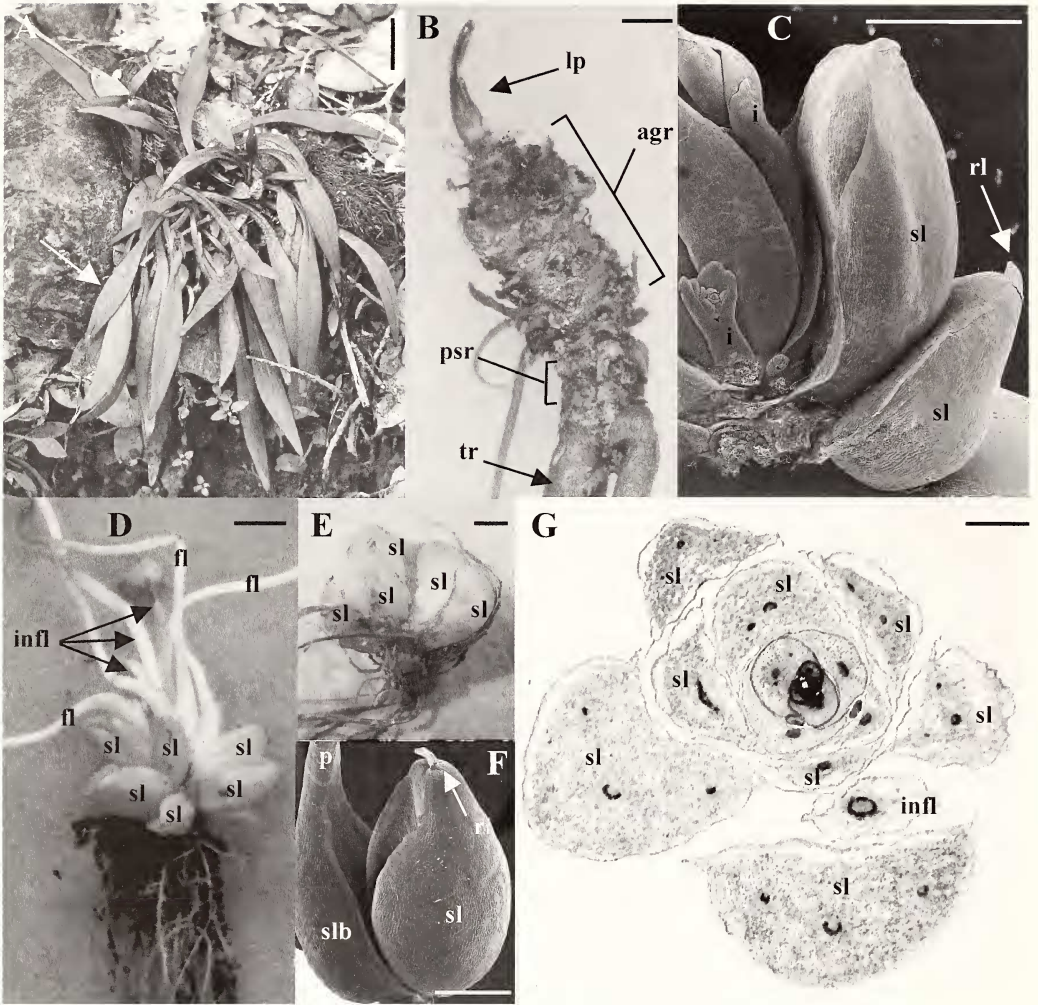
FIG 5.   Shoot system of *C. sibirica* var. *bulbillifera*. A. Habit. Arrow shows elliptical lamina of the foliage leaf. B. Dissected shoot system showing two seasons of growth. The stem is thicker in the region of active growth than for the preceding season. Foliage leaves, inflorescences and shoot-borne roots have been removed. C. Swollen scale leaves attached to distal portion of a rhizome. D. Shoot system showing overwintered scale leaves proximal to newly expanding foliage leaves and inflorescences. E. Subterranean bulb. F. Shoot system showing characteristics of transition from foliage to scale leaf zones. G. Cross section through distal portion of shoot showing transectional shape of scale leaves. agr = active growth rhizome, fl = foliage leaf, infl = inflorescence axis, lp = leaf primordium, p = petiole, psr = preceding season's rhizome, rl = rudimentary lamina, sl = storage leaf, slb = storage leaf base, tr = taproot. Scale bar = 1.0 cm in A; 2.0 mm in B, C, E; 5.0 mm in D; 1.0 mm in F, G.

inflorescences in the axils of the uppermost (Fig. 3C). Inflorescence axes have a subequal pair of oblanceolate to broadly elliptic leaves and flowers are subtended by small oblanceolate bracts. Under natural and greenhouse growth conditions, *C. palustris* has a size comparable to *C. sibirica* var. *bulbillifera*.

The axillary buds that become renewal shoots extend plagiotropically from the axils of rosette leaves and become highly elongated (5–15 cm) (Fig. 6D, E). Most of this elongation is in a single, basal internode (i.e., a hypopodium *sensu* Bell [1991]) that initially has a slightly swollen apical zone with unexpanded leaf primordia (Fig. 6E).

The apical zone, (Fig. 6A) which consists of few nodes, becomes orthotropic, undergoes radial thickening in the axis, and foliage leaves expand. Shoot-borne roots are formed at nodes of these swollen, orthotropic renewal shoots, which then replicate the architecture of primary shoots over the course of the growing season.

Modified Leaves

A heteroblastic shift from foliage leaves to scale leaves was observed in all examined ramets of *C. sibirica* var. *bulbillifera* (Figs. 3B, 5D, 7), but was uncommon among ramets of *C. sibirica*
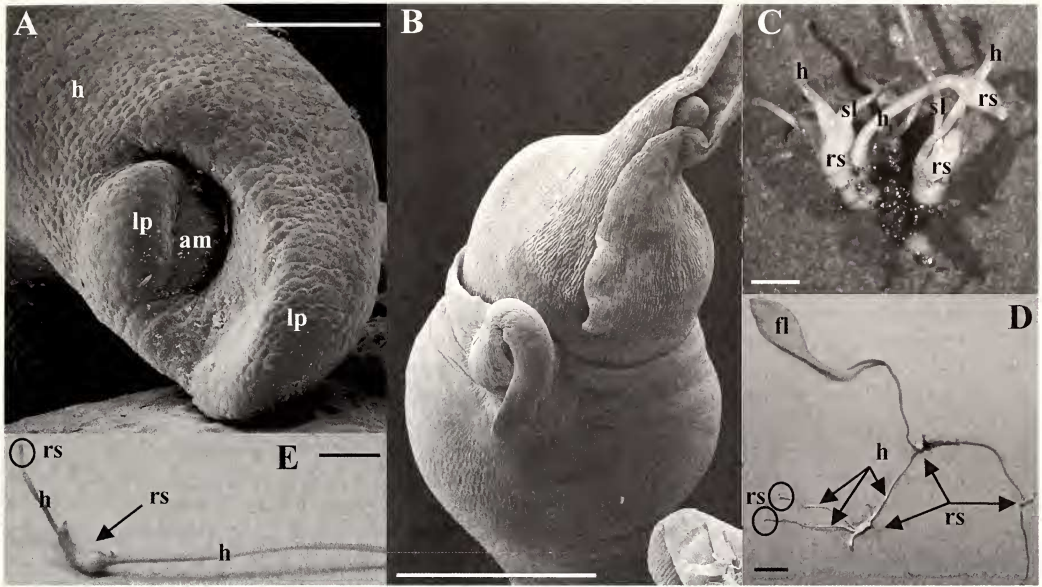
FIG. 6   Shoot system of *Claytonia palustris* A. Renewal shoot apex showing two leaf primordia at apical meristem. B. Renewal shoot showing prominently swollen axis apex. C. Renewal shoots. D. Stoloniferous habit. E. Renewal shoot with hypopodia. am = apical meristem, fl = foliage leaf, h = hypopodium, lp = leaf primordium, rs = renewal shoot, sl = scale leaf. Scale bars = 100 μm in A; 1.2 mm in B; 1.0 cm in D; 5 mm in C, E.

var. *sibirica*. The scale leaves of both varieties have rudimentary laminas that have a primordial shape and size and are frequently dislodged from the leaf base at maturity (Figs. 4D, G, 5C–F, 7A). All scale leaves are supplied by a single vascular strand, which broadens to form one medial and two lateral bundles that are embedded in a ground tissue of large, starch-filled, isodiametric cells. The epidermis is a single cell layer thick.

Scale leaf form, however, differs between the two varieties. Scale leaves of *C. sibirica* var. *sibirica* are similar in size and shape to the leaf bases of foliage leaves (Fig. 4D, F, G). In contrast, the scale leaves of *C. sibirica* var. *bulbillifera* are radially thicker than the bases of
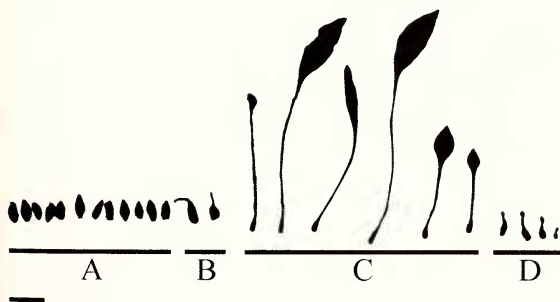

FIG. 7   Heteroblastic leaf series from one individual ramet of *Claytonia sibirica* var. *bulbillifera* (collected July 2004). A = Swollen scale leaves proximal to foliage leaves of the active growing season. B = Transition leaves with swollen bases, short petioles and small laminas. C = Foliage leaves. D = Swollen scale leaves at distal end of shoot.

most foliage leaves, although transitional leaf forms that had a thickened base, short petiole, and small lamina were found among early season foliage leaves directly preceding the formation of foliage leaves (Figs. 5F, 7D). The thickening of scale leaves of *C. sibirica* var. *bulbillifera* is centered primarily in cells adaxial to the primary vascular strand, producing a flattened adaxial surface (Fig. 5C, G). In constrast, scale leaves of *C. sibirica* var. *sibirica* had limited adaxial thickening and retained the adaxial concavity of foliage leaf bases (Fig. 4D–F). Modified leaves in the western morph of *C. sibirica* var. *sibirica* were found only in late season collections and always in the distal portion of the shoot. This contrasts with our observations of *C. sibirica* var. *bulbillifera*, in which the late-forming scale leaves (i.e., storage leaves) persisted through the winter attached to the stem axis and were subjacent to the expanding foliage leaves and inflorescences of the next growing season (Fig 5D).

DISCUSSION

Being a Bulb

Perennial members of the *C. sibirica* complex have similar globose to ovoid primary shoot axes that bear annually a basal rosette of leaves, from which axillary inflorescences and renewal shoots are formed (Fig. 3A–C). Although these shoot systems are fundamentally rhizomatous (*sensu* Bell 1991), some variants in the *C. sibirica* complex have been described as having bulbs,

bulblets, or bulbils, and being bulbiferous (Gray 1877, 1887; Miller et al. 1984). Thus, it is important to clarify the bulb aspects of shoot systems in the *C. sibirica* complex to understand how they represent modifications of the basic rhizomatous shoot system. Bulbs and bulblets are usually described as orthotropic shoot systems that bear fleshy (especially enlarged) scale leaves along very short internodes (Arber 1925; Rees 1972; Dahlgren and Clifford 1982; Bell 1991). Shoot systems of *C. sibirica* var. *bulbillifera* meet the criteria for bulb morphology. The production of relatively large, fleshy scale leaves between the cyclic intervals of reproductive growth seen in *C. sibirica* var. *bulbillifera* results in a bulb morphology that presumably serves as a perennation specialization of the basic rhizomatous form shared with other members of the complex. Gray's characterization of the KR form as having bulbs in a basal rosette (Gray 1877) and a crown of bulblet-scales (Gray 1887) calls attention to architectural variation: renewal shoots that formed in the axils of foliage leaves can have the form of bulbs when distal scale leaves swell late in the growing season and on the primary axis new succulent scale leaves of the current growing season would be formed as a crown distal to the foliage leaves. Bulbs of *C. sibirica* var. *bulbillifera* differ from those found commonly among various geophytic monocots. For example, geophytic monocots often have a thin, dry scale leaf or leaves (the tunic) that surrounds the entire bulb (Mann 1952; Rees 1972; McNeal and Ownbey 1973). Because they have very short internodes and leaves that lack petioles, it can appear that foliage leaves of geophytic monocots emerge from the rosette of fleshy scale leaves (Arber 1925; Dahlgren and Clifford 1982). Both of these distinctive aspects of monocotyledonous bulbs are lacking in *C. sibirica* var. *bulbillifera*, which has neither thin, dry scale leaves nor foliage leaves without petioles. Despite Dahlgren and Clifford's (1982) assertion that bulbs are a specialization found only in monocotyledons, we and others (Rees 1972; Cronquist 1981; Bell 1991), have recognized that a few clades of dicotyledons have also converged on bulb morphology.

Claytonia sibirica var. *bulbillifera* appears to be a serpentine endemic, and we hypothesize that the serpentine environment provided the selection for its bulb morphology. Kruckeberg (1984) discussed the general infertility of serpentine soils and the low turnover of nitrogen and phosphorus in communities associated with these soils. He emphasized that these unique nutritional and chemical characteristics have not only ecological but also evolutionary consequences, namely the origin of endemic species and subspecific ecotypes of plants adapted strictly to the serpentine environment. In the KR region, the growing season is limited largely to the late winter and spring and the above-ground foliage of herbaceous perennials has generally senesced by later summer. This relatively short growing season for herbaceous perennials in the KR is reminiscent of that faced by spring ephemerals of eastern deciduous forests. Lapointe (2001) emphasized that subterranean perennating structures, including bulbs, corms, thick rhizomes, and tubers, were evolutionary responses to the strong selection that spring ephemerals face for the rapid allocation of high levels of nutrients for shoot growth during the early spring when cool temperatures may limit enzymatic activity for photosynthesis. Herbaceous perennials of the KR region would face similar selection; moreover, this selection would be enhanced by the nutrient limitation of the serpentine environment. Thus, selection for a bulb morphology in this complex, in which ancestral heteroblastic variation would have included the formation of thick scale leaves as exemplified by *C. sibirica* var. *bulbillifera*, would help to circumvent the early season need for the rapid uptake of nutrients and augment the general nutrient-limited environment imposed by serpentine substrates by making nutrients available largely from scale leaves that are specialized for nutrient storage (and were provisioned over the course of the preceding growing season).

Morphological Transitions and Homology

Claytonia sibirica. Arber (1925) emphasized the morphological continuity between bulbs and rhizomes, and we observe this transition in *C. sibirica*. The shoot architecture of both varieties of *C. sibirica* is largely the same, but in var. *bulbillifera* we find specialization in the consistent formation of swollen scale leaves distal to the foliage leaves. At the end of the growing season, the bulb of var. *bulbillifera* consists of a tight aggregation of swollen storage leaves clustered around the preformed, but unexpanded, foliage leaves and inflorescences of the next growing season. Not all ramets of *C. sibirica* var. *sibirica* form scale leaves at the end of the growing season, but when scale leaves develop they have largely the size and shape of foliage leaf bases and are arranged in a relatively loose rosette at the tip of the shoot and are fewer in number than the swollen scale leaves of var. *bulbillifera* (cf. Fellows 1971). Given the positional and morphological similarity of scale leaves in both varieties, we hypothesize that they are homologous.

Miller et al. (1984) suggested that attributes of diploids, such as the morphotypes described here for varieties *sibirica* and *bulbillifera*, could have been combined in hybrid populations and this could account for the presence of scale leaves in some ramets of var. *sibirica*. Alternatively, the formation of scale leaves by some perennial

ramets of var. *sibirica* may simply represent variation in populations irrespective of hybridization or polyploidy. Instead these bulb-like modifications may be similar to the precursors of the distinctly bulbous var. *bulbillifera*. Additional populations of var. *sibirica* over its geographic range and habitat conditions need to be sampled for morphological variation, ploidy level, and ancestry to ascertain the phylogenetic homology of shoot system variants.

Claytonia palustris. In contrast to Miller's (1984) description of *C. palustris* as having "...branched rhizomes that are bulbiferous," we did not observe shoot systems in our sampling of this species that had the morphology of bulbs (cf. also Swanson and Kelley 1987). Primary and renewal axes of *C. palustris* become swollen and have short internodes that bear scale leaves at the end of the growth season, but these scale leaves do not enlarge as storage structures, a critical feature of bulbs. The initial elongation of axillary renewal shoots is centered in a single internode, a hypopodium (*sensu* Bell 1991), that functions in a manner similar to the droppers of various monocotyledonous geophytes, (e.g., *Erythronium*), in positioning the orthotropic portion of the renewal axis at a distance from the parent shoot (Arber 1925; McLean and Ivimey-Cook 1951). The hypopodia of *C. palustris* are homologous to the aerial rhizomes of other members of the *C. sibirica* complex but differ in the distance they remove renewal shoots from the parent plant. Aside from the formation of hypopodia during the initial elongation of renewal shoots, shoot architecture is very similar in *C. palustris* and *C. sibirica*. However, *C. palustris* is further distinguished from *C. sibirica* by the formation of leaf bases that completely ensheath the shoot axis, and these leaf bases lack the radial thickening that is common in *C. sibirica*.

Taxonomic Implications

Miller et al. (1984) did not recognize the morphotypes in the *C. sibirica* complex as different taxonomic entities, although they clearly describe morphological variation attributable to genetic differences. Chambers (personal communication) contends that *C. sibirica* exhibits a high degree of genetic variation over its wide latitudinal range but does not find clear delineations between types to warrant taxonomic recognition. However, plants cultivated from seed and grown over successive years under uniform greenhouse conditions show that plants from the KR maintain a strongly bulbiferous phenotype (O'Quinn unpublished data), from which we infer that shoot system plasticity in the formation of enlarged, fleshy scale leaves is limited. Because of their distinctive bulb morphology, discrete

geographic distribution and preference for serpentine soils, we have followed Gray's (1887) treatment in recognizing KR populations as *C. sibirica* var. *bulbillifera*.

LITERATURE CITED

ARBER, A. 1925. Monocotyledons: a morphological study. Cambridge University Press, Cambridge.

BELL, A. D. 1991. Plant form: an illustrated guide to flowering plant morphology. Oxford University Press, New York, NY.

CHAMBERS, K. L. 1993. *Claytonia*. Pp. 898–900 *in* J. C. Hickman (ed.), The Jepson manual: higher plants of California. University of California Press, Berkeley, CA.

CRONQUIST, A. 1981. An integrated system of classification of flowering plants. Columbia University Press, New York, NY.

DAHLGREN, R. M. T. AND H. T. CLIFFORD. 1982. The monocotyledons: a comparative study. Academic Press, London.

FELLOWS, C. E. 1971. A cytotaxonomic study of the origin of *Claytonia washingtoniana*. M.S. thesis. Humboldt State University, Arcata, CA.

GRAY, A. 1877. Characters of new species etc. Proceedings of the American Academy of Arts and Sciences 12:54.

———. 1887. Contributions to American Botany. XV. 1. Revision of some polypetalous genera and orders precursory to the Flora of North America. Proceedings of the American Academy of Arts and Sciences 22:270–314.

JOHANSEN, D. A. 1940. Plant microtechnique. McGraw-Hill Book Company, Inc., New York, NY.

KRUCKEBERG, A. 1984. California serpentines: flora, vegetation, geology, soils and management problems. University of California Press, Berkeley, CA.

LAPOINTE, L. 2001. How phenology influences physiology in deciduous forest spring ephemerals. Physiologia Plantarum 113:151–157.

MANN, L. K. 1952. Anatomy of the garlic bulb and factors affecting bulb development. Hilgardia 21:195–251.

MCLEAN, R. C. AND W. R. IVIMEY-COOK. 1951. Textbook of theoretical botany, Vol. 1. Longmans, Green and Company, London.

MCNEAL, D. W. AND M. OWNBEY. 1973. Bulb morphology in some western North American species of *Allium*. Madroño 22:10–24.

MILLER, J. M. 2003. *Claytonia* L. Pp. 485–488 *in* Flora of North America Committee, Flora of North America north of Mexico, Vol. 4 Magnoliophyta: Caryophillidae, pt 1. Oxford University Press, New York, NY.

————, K. L. CHAMBERS AND C. E. FELLOWS. 1984. Cytogeographic patterns and relationships in the *Claytonia sibirica* complex (Portulacaceae). Systematic Botany 9:266–271.

O'QUINN, R. L. AND L. HUFFORD. 2005. Molecular systematics of Montieae (Portulacaceae): implications for taxonomy, biogeography and ecology. Systematic Botany 30:314–331.

QUARTZ PCI, 1993–1998. Scientific Image Management Systems. Quartz Imaging Corporation. Version 4.20.

REES, A. R. 1972. The growth of bulbs. Academic Press, London.

SWANSON, J. R. AND W. A. KELLEY. 1987. *Claytonia palustris* (Portulacaceae), a new species from California. Madroño 34:155–161.